Bacterial complexity

Life on Earth depends on photosynthesis — the harvesting of light by organisms to draw CO_2 out of the air, and to harvest nutrients from the soil and water. The planet would otherwise be barren. Phytoplankton, in salt or freshwater, do fully half of that photosynthesis, fixing roughly 35–50 billion tons of carbon each year, and all this despite weighing, in the collective, 1,000 times less than land plants. Phytoplankton are secretly efficient photosynthesizers.

Thirty years ago, biologists thought these phytoplankton ranged in size from one millimetre to ten micrometres in diameter, with the smallest being a tenth the width of a human hair. But advancing technology soon uncovered a surprise — the bulk of oceanic photosynthesis actually depends on organisms ten times smaller. The bacterium *Prochlorococcus marinus* is the smallest photosynthetic organism known, at just 0.5 to 0.8 micrometres across, and is perhaps the most plentiful species on Earth. In 2013, researchers estimated that there are some 10^{27} such cells in the oceans, mostly near the surface, and they account, in some ocean regions, for as much as half of the total chlorophyll.

What makes this species important, however, isn't just its astonishing numbers. It's one of a number of bacteria that seem to break some of the fundamental rules of biology. Last month, biologist Sallie Chisholm of MIT gave the lead lecture at a three-day seminar on new directions in biology at the Carl Woese Institute for Genomic Biology at the University of Illinois. Her main message — echoed by the contributions of other participants (see http://conferences.igb.illinois.edu/woesenewbiology/) — was that we still have surprisingly large gaps in our understanding of life, and some of our basic ideas about species and genomes may be deeply flawed. *Prochlorococcus* is a prime example.

In the 1990s, Chisholm and her colleagues grew cultures from samples of ocean water taken from different depths, and first found two distinct 'ecotypes' — one adapted to the bright light very near the surface and another more suited to the low-light at deeper levels. This isn't so surprising, as many species have ecotypes adapted to slightly different environments — humans have different skin colours suited to local conditions, for example, and these reflect small genetic variations. However, the genetic differences in the *Prochlorococcus* ecotypes turn out to

For some organisms the idea of 'species' may not be a useful concept.

be much more profound — for example, each ecotype thrives in conditions under which the other would die.

When sequenced, the two ecotypes shared some 1,350 of the same genes, yet one ecotype had a total of 2,300 genes and the other only 1,700. Even the physical content of the DNA was markedly different. In one ecotype, the fraction of guanine-cytosine base pairs was 30%, whereas in the other it was 50%. Further study of the bacterium from oceans around the globe shows that these two ecotypes were only the beginning of a much deeper diversity. Researchers have now identified some 39 distinct strains from different habitats. They share about 1,200 'core' genes, yet show huge variations in other 'flexible' genes that vary with environment. Estimates put the total number of such genes in the complete *Prochlorococcus* group at around 80,000 — about three times the number of human genes (Stephen Biller *et al.*, *Nature Rev. Microbiol.* **13,** 13–27; 2015).

These flexible genes seem to code for specific useful features — extra cellular protection for cells thriving near the ocean surface, for example, or specific proteins useful for defence against viruses common to some oceanic zone. Large-scale meta-genomic studies of all the genetic content of different seawater samples showed that *Prochlorococcus* in the Atlantic Ocean have many more genes for phosphorous acquisition than do those in the Pacific Ocean. This makes sense, as the phosphorus concentration in the Atlantic is some ten times smaller.

At finer levels of detail the diversity is even more amazing. In a study published last year, researchers from Chisholm's lab have sampled individuals from the same millilitre of ocean water and found enormous diversity even there. Hundreds of sub-populations of organisms form clusters in genomic space, groups with similar 'backbones' of core genes decorated with particular sets of flexible genes. The broad ecotypes actually consist of more subtle sub-populations.

This spectacular diversity has another side to it. The basic core genes common to the entire *Prochlorococcus* group represent a kind of rudimentary genomic plan or simplified theme, with every actual organism being some considerable elaboration upon it. As a result, Chisholm suggests, understanding how *Prochlorococcus* thrives may require thinking about the 'genome' in a new way — and the species may not always be the right level for it. For example, another interesting fact about *Prochlorococcus* is that it enjoys the presence of other bacteria. Why? Well, the basic streamlined genome of *Prochlorococcus* lacks genes encoding the enzyme catalase, which almost all organisms use to break down the toxic chemical hydrogen peroxide. *Prochlorococcus* doesn't need this enzyme only because the other bacteria it maintains in its environment supply this enzyme themselves. In effect, *Prochlorococcus* uses the genomes of other organisms. Put another way, it's as if metabolic coherence doesn't exist just at the level of the single cell, but at the level of an interacting group of organisms of many different species.

One further oddity — *Prochlorococcus* plays host to a variety of infecting viruses, which, coincidentally, carry many genes that are very close to many *Prochlorococcus* genes. Why would they do that? Again, Chisholm points to a rather unusual kind of symbiosis. These viruses seem to be vehicles for ferrying genes between distinct *Prochlorococcus* organisms. So, although we're used to thinking of the interaction of virus and host as a win–loss relationship, here it seems that both gain. Indeed, it's more like the viruses are part of a larger coherent system or meta-population of organisms. The viruses help maintain genetic diversity and, possibly, help improve the fitness of the larger complex.

These are a few of the surprises linked to a bacterium that was unknown just 30 years ago. *Prochlorococcus* looks like a signpost pointing biology toward its next challenge — to move beyond the idea of 'species', which may not be a useful concept for some organisms. *Prochlorococcus* can't be understood by studying a single copy, a single cell, the details of which in no way reflect the diversity of the entire collection. The organism, it seems, can't even be understood without reference to its environment, and the close interactions it has with many other species. ❐

MARK BUCHANAN

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